Forest management treatments, tree resistance, and bark beetle resource utilization in ponderosa pine forests of northern Arizona

Kimberly F. Wallin [a,*], Thomas E. Kolb [b,1], Kjerstin R. Skov [c], Michael Wagner [b]

[a] The Rubenstein School of Environment and Natural Resources, University of Vermont, 321 Aiken Center, Burlington, VT 05404, United States
[b] School of Forestry, Northern Arizona University, P.O. Box 15018, Flagstaff, AZ 86011-5018, United States
[c] USDA Forest Service, Forest Health Protection, Ogden, UT, United States

Abstract

We show experimentally that forest restoration treatments that used thinning to reduce ponderosa pine density near Flagstaff, Arizona decreased the percentage of trees with successful bark beetle attacks induced by beetle community response to a *Dendroctonus brevicomis* pheromone. Underlying mechanisms for the beneficial effect of restoration treatments on tree resistance to bark beetles included stimulation of resin defenses. Resin flow after phloem wounding was greater in full and partial restoration treatments than the control in the first and second year after treatment. Five bark beetle species, *Ips pini*, *D. brevicomis*, *D. valens*, *D. adjunctus*, and *D. frontalis*, colonized and produced brood in the trees. There was a negative correlation between resin volume and number of brood that emerged from the bole. Niche breadth of the bark beetle species over bole positions was widest for *I. pini* and narrowest for *D. brevicomis*.
© 2008 Elsevier B.V. All rights reserved.

1. Introduction

Thinning densely stocked stands of suppressed trees followed by prescribed fire is commonly used as a restoration treatment in forest ecosystems that are adapted to frequent, low-intensity fire (e.g., Covington et al., 1997; Moore et al., 2004). Restoration treatments that use thinning and prescribed burning have been shown to stimulate resource uptake and growth of ponderosa pine (*Pinus ponderosa*) in the Southwest U.S. (Schubert, 1974; Kolb et al., 1998; Zausen et al., 2005; McDowell et al., 2006). Such treatments have been reported to increase production of carbon-based defenses against bark beetles, such as resin, in some (Kolb et al., 1998; Feeney et al., 1998; McDowell et al., 2007), but not all (Zausen et al., 2005) studies. However, few studies have explored the effects of restoration treatments on bark beetle colonization, impacts of increased resin volume on brood production of beetles, and within-tree resource utilization.

Ponderosa pine forests support complex communities of bark beetles (Coleoptera: Curculionidae, Scolytinae) (D.L. Wood, 1982; Gaylord et al., 2006). Bark beetle success is influenced by dynamic interactions with host trees and local populations of conspecifics (Lanier and Wood, 1975; Lanier et al., 1980). The effects of these interactions on bark beetle success likely shifts with changes in host defenses and density of local beetle populations. For example, at endemic population levels, beetles primarily attack less vigorous trees (Wallin and Raffa, 2005). However, beetles will attempt to colonize vigorous trees as conspecifics and other biotic agents deplete less vigorous trees (Berryman, 1982). Bark beetles emit pheromones to attract mates and coordinate mass attacks that can overcome defenses, such as resin (Rudinsky, 1962; Borden, 1982; S.L. Wood, 1982).

Bark beetle aggregation pheromones attract conspecifics, mates, and inter-specifics (Gaylord et al., 2006). Multiple species of bark beetles may respond to these pheromones and live and breed within the phloem tissue of the same tree species and even the same tree (Paine et al., 1981; Smith et al., 1990). Intra- and inter-specific competition for food and space frequently limits

bark beetle reproductive success (Borden et al., 1993). However, the costs of competition may be offset by the benefit of entry by a large number of beetles within a short time frame that can exhaust host defenses (D.L. Wood, 1982; Raffa and Berryman, 1983; Robins and Reid, 1997; Raffa, 2001). In addition, inter-specific competition can be lessened by varied resource utilization patterns, or niche differentiation among beetles, within a single host tree (Birch, 1978; Paine et al., 1981; Wagner et al., 1985; Haack et al., 1987; Amezaga and Rodriguez, 1998; Ayres et al., 2001).

The occurrence and importance of synchronized attacks by bark beetles in overcoming host defenses in southwestern ponderosa pine forests are poorly understood. In these forests *Dendroctonus adjunctus* and *D. valens* often occur from the base of the tree to 0.5 m in height. *D. brevicomis* and *D. frontalis* are found in mixed assemblages from the base to 2.0 m or more in height tree (Breece et al., 2008). *Ips pini* are generally found above 2.0 m in height (Breece et al., 2008), or where bark is thin (Kolb et al., 2006). Beetle success in killing a vigorous host by a synchronized attack could offset costs of inter-specific competition. Alternatively, niche overlap of two or more species may prevent an individual species from ever dominating utilization of the resource and reaching outbreak levels.

Restoration treatments that consisted of tree thinning and prescribed burning of logging slash increased water uptake, photosynthesis, and radial growth of ponderosa pine at our study site in northern Arizona (Skov et al., 2004, 2005). Our study addresses the influence of these restoration treatments on ponderosa pine resistance to bark beetles for the first and second post-treatment years. We measured tree resistance to bark beetles as resin volume after phloem wounding, number of successful attacks, and by the relationship between resin flow and beetle brood production. Because bark beetle populations were at endemic levels during the study, we collected attack data with and without the use of pheromone lures placed on trees. A secondary goal was to describe resource utilization and niche partitioning within the tree for the bark beetle community that included five beetle species at our study site.

2. Materials and methods

2.1. Study site

The study site was the Fort Valley Experimental Forest located approximately 10 km NW of Flagstaff, AZ (35°15′58″N lat. and 111°42′13″W long.; or zone 48, 500,000 m east, 3,873,043 m north; elevation 2200 m). Annual precipitation averages 570 mm with about half occurring as winter snow and half as late-summer rain (Western Regional Climatic Center: http://www.wrcc.dri.edu/index.hmtl). Soils are derived from basalt and are classified as a fine montmorillonitic complex of frigid Typic Argiborolls and Mollic Eutroboralfs (Miller et al., 1999). The frost-free season in the region of the study sites averaged 94 days (Schubert, 1974). Tree composition at the site was dominated by ponderosa pine, which was 99.8% of all trees (Skov et al., 2005).

The restoration treatments (described in detail in Skov et al., 2005) occurred between December 1998 and September 1999 and used tree thinning to experimentally establish four levels of tree density. All thinning treatments were followed by prescribed burning of logging slash in 1999 or 2000. We included three levels of tree density in this study and each level was replicated twice spatially by a 17 ha plot.

The three treatments used in our study were full restoration, partial restoration, and control. No old trees (estimated age > 150 years, diameter at breast height (dbh) > 54 cm, having yellow bark) were cut in the thinned treatments. All younger trees were cut, except for trees that were retained when nearby there was evidence (stumps, stump holes, snags, down logs) of dead trees (following Covington et al., 1997 and described in detail in Skov et al., 2005). The full and partial restoration treatments differed only in the number of trees that were retained to replace old, dead trees. The full restoration treatment replaced each pre-settlement tree with an average of 1.5 trees $\geq$ 40 cm dbh, or three trees < 40 cm when larger trees were not available. The full restoration treatment reduced average basal area by 58% (38–16 $m^2\ ha^{-1}$) and average tree density by 85% (966–142 trees ha^{-1}). The partial restoration treatment used replacement levels of three larger or six smaller trees for each evidence of an old tree, and reduced average basal area by 35% (34–22) and average tree density by 77% (1055–245 trees ha^{-1}) (Skov et al., 2005). Basal area of the unthinned, control treatment averaged 38 $m^2\ ha^{-1}$ and tree density averaged 1201 trees ha^{-1} (Skov et al., 2005).

2.2. Tree resin defense response to restoration treatments

Tree resin flow after phloem wounding and prior to colonization by subcortical insects was used as a measure of resistance against bark beetles. We sampled 12 trees per treatment and per replication, totaling 72 trees, during pre- (June) and post- (August) monsoon seasons in years 2000 and 2001. Each sampled tree had a diameter 1.4 m from the base of the tree between 23 and 29 cm. Resin flow was measured using methods of Lorio (1993). The outer bark was removed with a drawknife, and the remaining bark and phloem were punctured with a 2.5-cm-diameter arch punch, avoiding injury to xylem. Aluminum troughs were pinned to the bark below the wound and resin was channeled into a graduated tube (Lorio, 1993; Kolb et al., 1998; Wallin and Raffa, 2001). After 24-h, the vials were removed and total volume was measured to the nearest 0.1 ml.

We compared resin flow among treatments in each year with a fixed-effects ANOVA model using ANOVA and SAS JMP software (SAS, 1996) that included thinning treatment, season (June and September), and their interaction as factors. Variances were homogeneous among treatments and dates as indicated by Levene's test (Sokal and Roalf, 1995). Mean comparisons among treatments and months with a year were performed with Fisher's protected LSD at $p = 0.05$.

2.3. Bark beetle colonization and resource utilization

We visually assessed the bole of the 72 trees that were sampled for resin flow, plus an additional 72 similar-size trees (12 per treatment per replication), for the presence of bark beetles in 2000 and 2001. During beetle flight, the entire length

of the bole (from the base of the tree to the base of the canopy) of each of the 144 trees was examined weekly until new colonization attempts came to an end in 2001. We counted the total number of trees that were successfully colonized by bark beetles, and distinguished unsuccessful and successful attempts at colonization. Unsuccessful attempts had pitch tubes with beetles trapped within resin and no visible frass. Successful attempts had pitch tubes without trapped beetles and frass was present.

Because insect population densities were low, we promoted colonization in the second year of the study (2001) using the synthetic pheromone lure for *D. brevicomis*. Each lure consisted of exo-brevicomin and frontalin with release rates of 4.1-µg day^{-1} and 0.86-µg day^{-1}, respectively (Phero Tech., Inc., Delta, BC, Canada). One lure was attached 2.0-m above the base to each of an additional 15 randomly selected trees (23–29 cm dbh) per treatment and per replication (90 trees total) in June 2001 immediately after measurement of resin volume. The pheromone lure was removed at the onset of successful colonization. We quantified bark beetle attacks as described above.

We quantified brood production of bark beetles in all trees that were successfully colonized. All of the successfully colonized trees were baited with the *D. brevicomis* lure in June 2001. Each tree was felled in September 2001 and sectioned into three 0.3-m sections that were sampled 0.3-, 3.0-, and 4.0-m from the base of the tree. Each section was placed in a nylon cloth emergence bag, sealed, and held at 22 °C in the laboratory. Emerged beetles were collected and identified to species until emergence ceased for three weeks.

We measured how different bark beetle species utilized the successfully colonized trees by using bole section as the resource parameter to calculate niche attributes of each species. We used formulas that have been used in similar ecological studies of bark beetles (Paine et al., 1981; Schyter and Anderbrant, 1993). The extent to which each species used different bole sections was calculated as Levins niche breadth (1968),

$$B = \frac{1}{\sum p_{ij}^2}$$

where B = niche breadth, p_{ij} is the proportion of the species found in the jth section category and i is the number of sections. Interaction between species was estimated by Levins (1968) formula for niche overlap,

$$\alpha_{ij} = \sum p_{ih} p_{jh}(B_i)$$

where α_{ij} is niche overlap for species i and j, p_{ih} and p_{jh} are the proportions of each species in the hth bole section, and B_i is the niche breadth of species i. The similarity between the distributions of two species in a section was quantified as proportional similarity,

$$C_{ij} = 1 - \frac{1}{2} \sum |p_{ih} - p_{jh}|$$

where C_{ij} = proportional similarity for species i and j, p_{ih} and p_{jh} are the proportions of species i and j, respectively, in the hth bole section. Comparisons of niche overlap among species pairs were preformed using the bole section average for each insect pair at each replication of each treatment. We used a proportional similarity coefficient <0.7 as the cut-off point for segregated species (Hutchinson, 1959). We used t-tests with Bonferroni adjusted alpha levels of 0.0125 for comparisons of niche breadth and 0.005 for comparisons of niche overlap among bark beetle species. To increase their homoscedasticity, data on niche breadth and niche overlap were log-transformed before analysis (SAS, 1996). Non-transformed data are presented for clarity. ANOVA was used to analyze the niche breadth data for differences among species, and mean comparisons were made using Fisher's protected LSD.

3. Results

3.1. Tree resin defense response to restoration treatments

In June 2000, trees in the full restoration treatment had greater resin volume compared with trees in the partial restoration treatment and control (d.f. = 2, F = 4.6, $p < 0.01$) (Fig. 1). However, in August 2000 there were no significant differences in resin volume among treatments. Trees produced more resin in June than August of 2000 for all treatments (d.f. = 1, F = 5.2, $p < 0.01$). In June 2001, resin volume was higher in the full restoration treatment compared with the partial treatment and control (Fig. 1). In August 2001, resin volume was greater in the partial restoration treatment than the full treatment and control (Fig. 1). Also in 2001, resin volume was greater in June than August for trees in the control and full restoration treatment, whereas there was no difference between months for trees in the partial restoration treatment. In general,
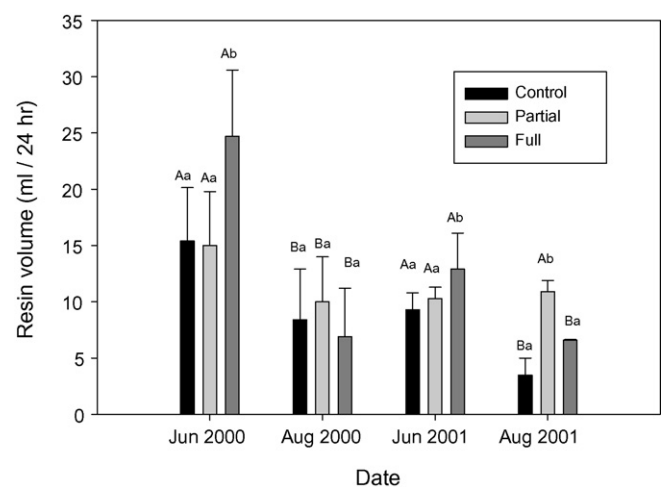

Fig. 1. Mean resin volume in the first 24 h after phloem wounding of ponderosa pine in two restoration treatments (partial, full) and an untreated control in June and August of 2000 and 2001. Bars indicate one standard error of the mean. Different capital letters above the bars indicate significant ($p < 0.05$) differences between months within treatments for each year, and different lowercase letters indicate significant differences among treatments within months and year based on mean comparisons with Fisher's protected LSD at $p = 0.05$.

resin volume was greater in 2000 than 2001 (d.f. = 1, $F = 4.8$, $p < 0.05$) (Fig. 1).

3.2. Bark beetle colonization and resource utilization

There were no successful attacks of trees lacking pheromone lures in all treatments in both years of the study. Only 47 of the 90 trees that were baited with pheromone lures in June 2001 had colonization attempts by bark beetles. Colonization attempts occurred on 30 of 30 trees (100%) in the control treatment, 15 of 30 trees (50%) in the partial restoration treatment, and 2 of 30 trees (7%) in the full restoration treatment (Fig. 2). All of the trees in the control were successfully colonized whereas 10 of the 30 trees (33.3%) in the partial restoration treatment were successfully colonized. The full restoration treatment had the least number of successful colonization attempts with 1 of the 30 trees (3%) having successful colonization (Fig. 2).

The subcortical insects that emerged from the trees included, in decreasing order of abundance, *I. pini*, *D. brevicomis*, *D. valens*, *D. adjunctus*, and *D. frontalis* (Table 1). *I. pini* was the only species that emerged from all sections of the bole (Table 1). There was significant overlap in occurrence between *I. pini* and *Dendroctonus* spp. within middle sections of the bole as shown by the frequent occurrence of proportional similarity coefficients greater than 0.70 indicating aggregation among species (Table 2).

Only *I. pini* emerged from the upper bole section and therefore it was segregated from the other four bark beetle species at this section (Table 2). *D. adjunctus* was segregated from *I. pini*, *D. brevicomis*, and *D. frontalis* in the middle section as indicated by the low coefficient of proportional similarity (Table 2). However, *D. adjunctus* was aggregated with *D. valens* in the middle and lower bole sections (Table 2). In the lower bole section all species pairs, with the exception of *D. valens* and *D. adjunctus,* were segregated from each other (Table 2).

Niche breadth differed significantly among species ($F_{1,170} = 63.65$, $p < 0.01$) (Table 3). *I. pini* had the greatest niche breadth and utilized all bole sections. In general, the

results on segregation between species within each bole section (Table 2) are consistent with differences in niche breadth (Table 3). For example, *D. brevicomis* emerged only from the middle bole section, and *I. pini* was the only beetle species that emerged from upper bole section (Tables 1–3).

Brood production, as measured by the number of emerging beetles from stem sections pooled over each tree with successful colonization, was negatively related to resin volume measured *in situ* just prior to attraction of bark beetles to the trees with the pheromone lures (Fig. 3). The negative relationship occurred both within each of the partial restoration treatment and control, and for data pooled over all treatments (Fig. 3).

4. Discussion

A major finding of our study is that restoration treatments that caused large reductions in tree density increased resin defenses of ponderosa pine in the first 2 years after treatment. When differences in resin flow in response to phloem wounding occurred, resin flow was greater in the full restoration treatment (June 2000 and 2001) or partial restoration treatment (August 2001) compared with the control. The same restoration treatments increased tree water uptake and photosynthesis, especially during drought (Skov et al., 2004), and also increased tree radial growth (Skov et al., 2005). These findings along with our results suggest that the restoration treatments reduced resource competition among trees and hence, tree stress, and increased carbon allocation to resin defenses in the tree bole. This interpretation is consistent with two other experimental thinning studies (Kolb et al., 1998; Wallin et al., 2004) and recent results of a region-wide synthesis for northern Arizona that showed a negative relationship between stand basal area and resin flow, and a positive relationship between tree radial growth and resin flow (McDowell et al., 2007).

There were no colonization attempts by bark beetles in any of the treatments in 2000 or 2001 without synthetic pheromone lures. This low level of activity was likely due to low populations of bark beetles in the area. The slash and burning caused by the restoration treatments apparently did not attract enough beetles into the stands to coordinate an attack effort in the absence of pheromone lures.

The *D. brevicomis* lure attracted several bark beetle species to trees in our study. All of the trees in the control and half in the partially restored treatment baited with the pheromone lure had colonization attempts. The control stands had more successful attacks than partially restored stands. Assuming similar beetle populations in each treatment, one explanation for this difference in colonization attempts is that the pheromone plume from the lure dispersed faster in the more open, thinned stands compared with the dense control stands (Thistle et al., 2004). This explanation is consistent with greater captures of *D. brevicomis* in pheromone-baited funnel traps in dense, unthinned stands than thinned stands in another study in northern Arizona (Zausen et al., 2005).

The restoration treatments also reduced the percentage of trees with successful attacks in which beetle feeding occurred
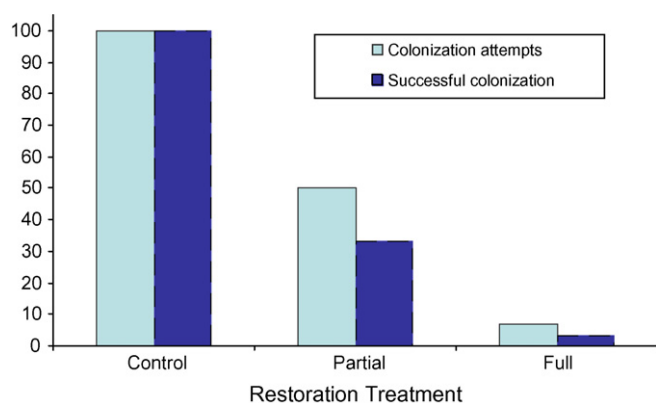

Fig. 2. Percentage of trees in two restoration treatments (partial, full) and the untreated control with bark beetle colonization attempts and successful colonization. All of the trees were baited with *D. brevicomis* pheromone lure in June 2001. We counted attempts and determined success in late fall 2001.

Table 1
Mean and one standard error of the number of bark beetles (#/m^2 of bark surface) of five species that emerged from each vertical position along tree bole of colonized trees in control and partial restoration treatments

Bark beetle species	Vertical position along tree bole and treatment					
	Lower (0.3–0.6 m)		Middle (3.0–3.3 m)		Upper (4.0–4.0 m)	
	Control	Partial	Control	Partial	Control	Partial
I. pini	18.4 (5.3)	13.7 (12.3)	12.3 (48.2)	18.5 (97.3)	17.6 (17.4)	28.5 (14.9)
D. brevicomis	0	0	25 (50.1)	19 (67)	0	0
D valens	9.8 (69.4)	9.6 (35.2)	2.1 (14)	0.3 (1)	0	0
D. adjunctus	5.9 (69)	3.1 (22)	18 (10.2)	0	0	0
D. frontalis	18.2 (14.0)	6.3 (12.1)	5.5 (15.6)	2.5 (12.3)	0	0

N = 47 trees.

in the tree phloem. A lower percentage of successful attacks in the thinned, restoration sites may have resulted from failure of beetles to locate the pheromone source because of rapid dispersal of the plume (Thistle et al., 2004). Concentrated pheromone plumes in the dense, control stands may have attracted enough beetles for a successful mass attack that overcame tree defenses. Another explanation is that trees in the restoration treatments were able to quickly halt colonization of

Table 2
Coefficient of proportional similarity in distribution within bole sections between pairs of bark beetle species

Bole section	Beetle species pair	Proportional similarity	Segregation
Upper	V/A	N/A	+
	V/B	N/A	+
	V/F	N/A	+
	V/I	0.1	+
	A/B	N/A	+
	A/F	N/A	+
	A/I	0.1	+
	B/F	N/A	+
	B/I	0.1	+
	F/I	0.1	+
Middle	V/A	0.7	−
	V/B	0.7	−
	V/F	0.8	−
	V/I	0.8	−
	A/B	0.4	+
	A/F	0.4	+
	A/I	0.4	+
	B/F	0.8	−
	B/I	0.8	−
	F/I	0.9	−
Lower	V/A	0.8	−
	V/B	0.4	+
	V/F	0.4	+
	V/I	0.48	+
	A/B	0.1	+
	A/F	0.1	+
	A/I	0.1	+
	B/F	0.1	+
	B/I	0.1	+
	F/I	0.1	+

Segregation was assumed to occur (+) when the coefficient of proportional similarity was lower than 0.7 and aggregation (−) was assumed to occur when the coefficient was 0.7 or greater. Bark beetle species are coded as: V = *D. valens*, A = *D. adjunctus*, B = *D. brevicomis*, F = *D. frontalis*, and I = *I. pini*.

the pioneer beetle because of increased resin flow compared with trees in the control stands. The strong negative relationship between number of emerging brood beetles and resin flow that was derived from only trees with apparently successful colonization by beetles (Fig. 3) support a role of resin defenses in limiting beetle success.

The complex of bark beetles colonized the tree bole in our study consistent with niches recognized in previous reports (Birch, 1978; Biondi, 1996; Paine et al., 1981; Wagner et al., 1985; Ayres et al., 2001). There was overlap in resource use by beetle species in the middle section of the bole as shown by frequent aggregation in Table 2. *I. pini* was the most abundant species and was present in all sections of the bole, but the number of *I. pini* that emerged from the middle section was less than the upper section (Table 1). This result may have been caused by high inter-specific competition for space for brood production and development in the middle bole section (Reeve et al., 1998).

The *D. brevicomis* pheromone attracted several bark beetle species. This finding is consistent with the overlaps in flight periodicity previously reported for bark beetle species in northern Arizona (Gaylord et al., 2006). We speculate from these observations that aggregation pheromones from one bark
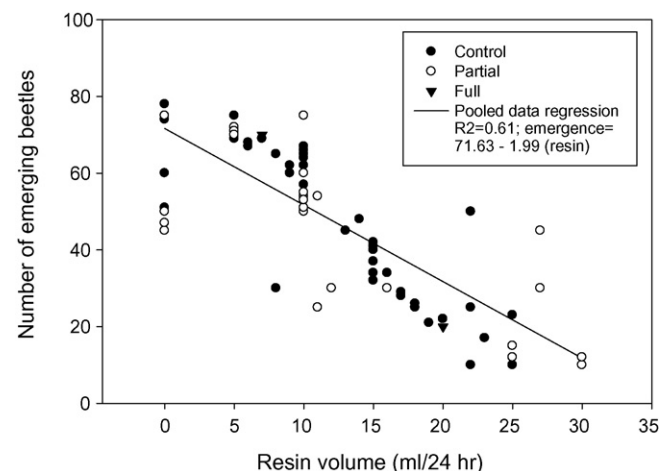

Fig. 3. Number of bark beetles pooled over beetle species that emerged from all ponderosa pine bole sections versus resin volume per tree collected the first 24 h after phloem wounding prior to colonization. Emergence data is shown for two restoration treatments (partial, full) and an untreated control. We used linear regression of emergence against resin flow on data pooled over all treatments.

Table 3
Mean niche breadth (±S.E.) for bark beetle species colonizing ponderosa pine trees with pheromone lures at upper, middle, and lower vertical bole sections

| Bark beetle species | Vertical position along tree bole | | | | | |
| | Lower (0.3–0.6 m) | | Middle (3.0–3.3 m) | | Upper (4.0–4.3 m) | |
	Mean	S.E.	Mean	S.E.	Mean	S.E.
I. pini	2.38[*]	0.13	2.74	0.20	2.82	0.15
D. brevicomis	–	–	3.17[*]	0.23	–	–
D. valens	1.4	0.16	2.04	0.13	–	–
D. adjunctus	1.87	0.10	1.16	0.18	–	–
D. frontalis	1.37	0.10	1.86	0.15	–	–

One asterisk following the mean indicates significant differences among species within bole section at 0.05 using Fisher's protected LSD.

beetle species, in this case *D. brevicomis*, trigger attacks by several other species on different parts of the bole, and these collective attacks overwhelm tree defenses.

In summary, we show experimentally that forest restoration treatments that use thinning to reduce tree density decreases the percentage of trees with successful bark beetle attacks induced by beetle community response to a *D. brevicomis* pheromone. Our study provides evidence of the positive effects of thinning in the context of forest restoration treatments on ponderosa pine resistance to lethal bark beetle attacks. Underlying mechanisms for the beneficial effect of restoration treatments on tree resistance to bark beetles included stimulation of resin defenses.

Acknowledgments

References

Amezaga, I., Rodriguez, M.A., 1998. Resource partitioning of four sympatric bark Beetles depending on swarming dates and tree species. Forest Ecol. Manage. 10, 127–135.

Ayres, B.D., Ayres, M.P., Abrahamson, M.D., Teale, S.A., 2001. Resource partitioning and overlap in three sympatric species of *Ips* bark beetles (Coleptera: Scolytidae). Oecologia 128, 443–453.

Biondi, F., 1996. Decadal-scale dynamics at the Gus Pearson Natural Area: evidence for inverse (a)symmetric competition? Can. J. Forest Res. 26, 1397–1406.

Birch, M.C., 1978. Chemical communications in pine bark beetles. Am. Sci. 66, 409–419.

Borden, J.H., Chong, L.J., Lindgren, B.S., Begin, E.J., Ebata, T.M., Maclauchlan, L.E., Hodgkinson, R.S., 1993. A simplified tree bait for the mountain pine beetle. Can. J. Forest Res. 23, 1108–1113.

Breece, C.R., Kolb, T.E., Dickson, B.G., McMillin, J.D., Clancy, K.M., 2008. Prescribed fire effects on bark beetle activity and tree mortality in southwestern ponderosa pine forests. Forest Ecol. Manag. 255, 119–128.

Covington, W.W., Fule, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sackett, S.S., Wagner, M.R., 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. J. Forestry 95, 23–29.

Feeney, S.R., Kolb, T.E., Wagner, M.R., Covington, W.W., 1998. Influence of thinning and burning thinning treatments on presettlement ponderosa pines at the Gus Pearson Natural Area. Can. J. Forest Res. 28, 1295–1306.

Gaylord, M.L., Kolb, T.E., Wallin, K.F., Wagner, M.R., 2006. Seasonality and lure preference of bark beetles (Curculionidae: Scolytinae) and associates in a Northern Arizona Ponderosa Pine Forest. Environ. Entomol. 35, 37–47.

Haack, R.A., Wilkinson, R.C., Foltz, J.L., Corniel, J.A., 1987. Spatial attack pattern, reproduction and brood development of *Ips calligraphus* (Coleoptera: Scolytidae) in relation to slash pine phloem thickness: a field study. Environ. Entomol. 16, 428–436.

Kolb, T.E., Guerard, N., Hofstetter, R.W., Wagner, M.R., 2006. Attack preference of *Ips pini* on *Pinus ponderosa* in northern Arizona: tree size and bole position. Agric. Forest Entomol. 8, 2985–3303.

Kolb, T.E., Holmberg, K.M., Wagner, M.R., Stone, J.E., 1998. Regulation of ponderosa pine foliar physiology and insect resistance mechanisms by basal area treatments. Tree Physiol. 18, 375–381.

Lanier, G.N., Wood, D.L., 1975. Specificity of response to pheromones in the genus *Ips* (Coleoptera: Scolytidae). J. Chem. Ecol. 1, 9–23.

Lanier, G.N., Classon, A., Stewart, T., Piston, J.J., Silverstein, R.M., 1980. *Ips pini:* the basis for inter populational differences in pheromone biology. J. Chem. Ecol. 6, 677–688.

Levins, R., 1968. Evolution in Changing Environments. Princeton University Press, Princeton, NJ.

Lorio Jr., P.L., 1993. Environmental stress and whole-tree physiology. In: Schowalter, T.D., Filip, G.M. (Eds.), Beetle-pathogen Interactions in Conifer Forests. Academic Press, London, pp. 81–101.

McDowell, N.G., Adams, H.D., Bailey, J.D., Hess, M., Kolb, T.E., 2006. Homeostatic maintenance of ponderosa pine gas exchange in response to stand density changes. Ecol. Appl. 16, 1164–1182.

McDowell, N.G., Adams, H.D., Bailey, J.D., Kolb, T.E., 2007. The role of stand density on growth efficiency, leaf area index and resin flow in southwestern ponderosa pine forests. Can. J. Forest Res. 37, 343–355.

Moore, M.M., Huffman, D.W., Fulé, P.Z., Covington, W.W., Crouse, J.E., 2004. Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. Forest Sci. 50, 162–176.

Paine, T.D., Birch, M.C., Svihra, P., 1981. Niche breadth and resource partitioning by 4 sympatric species of bark beetles (Coleoptera: Scolytidae). Oecologia 48, 1–6.

Raffa, K.F., 2001. Mixed messages across multiple trophic levels: the ecology of bark beetle chemical communication systems. Chemoecology 11, 49–65.

Raffa, K.F., Berryman, A.A., 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). Ecol. Monogr. 53, 27–49.

Reeve, D., Rhodes, D.J., Turchin, P., 1998. Scramble competition in the southern pine beetle, *Dendroctonus frontalis*. Ecol. Entomol. 23, 433–443.

Robins, G.L., Reid, M.L., 1997. Effects of density on the reproductive success of pine engravers: is aggregation in dead trees beneficial? Ecol. Entomol. 22, 329–334.

Schubert, G.H., 1974. Silviculture of Southwestern Ponderosa Pine: The Status-Of-Our-Knowledge. USDA Forest Service Rocky Mountain Forest Range Experiment Station. Paper Number RM-RP-123.

Skov, K.R., Kolb, T.E., Wallin, K.F., 2004. Tree size and drought affect ponderosa pine physiological response to thinning and burning treatments. Forest Sci. 50, 81–91.

Skov, K.R., Kolb, T.E., Wallin, K.F., 2005. Difference in radial growth response to restoration thinning and burning treatments between young and old ponderosa pine in Arizona. West. J. Appl. Forestry 20, 36–43.

Smith, M.T., Payne, T.L., Birch, M.C., 1990. Olfactory-based behavioral interactions among five species in the southern pine bark beetle group. J. Chem. Ecol. 16, 3317–3332.

Sokal, R.R., Roalf, F.J., 1995. Biometry; The Principles and Practice of Statistics in Biological. Freeman, New York.

Statistical Analysis Systems, 1996. Language and Procedures. Version 6 Cary, NC.

Thistle, H.W., Peterson, H., Allwine, G., Lamb, B., Strand, T., Holstein, E.H., Shea, P.J., 2004. Surrogate pheromone plumes in three forest trunk spaces: composite statistics and case studies. Forest Sci. 50, 610–625.

Wagner, T.L., Flamm, R.O., Coulson, R.N., 1985. Strategies for Cohabitation Among the Southern Pine Bark Beetle Species: Comparisons of Life-Process Biologies. USDA Forest Service General Technical Report SO-56, pp. 87–101.

Wallin, K.F., Kolb, T.E., Skov, K.R., Wagner, M.R., 2004. Seven year influence of thinning and burning restoration treatments on pre-settlement ponderosa pines at Gus Pearson Natural Area. Restor. Ecol. 12, 239–247.

Wallin, K.F., Raffa, K.F., 2001. Effects of folivory on subcortical plant defenses: can defense theories predict interguild processes? Ecology 82, 1387–1400.

Wood, D.L., 1982. The role of pheromones, kairomones and allomones in the host selection and colonization behavior of bark beetles. Annu. Rev. Entomol. 27, 411–446.

Wood, S.L., 1982.The bark beetles and ambrosia beetles of North America and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Naturalist Memoirs. Number 6. Brigham Young University, Provo, Utah.

Zausen, G.L., Kolb, T.E., Bailey, J.D., Wagner, M.R., 2005. Long-term impacts of stand management on ponderosa pine physiology and bark beetle abundance in northern Arizona: a replicated landscape study. Forest Ecol. Manage. 218, 291–305.